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N400 processes inhibit inappropriately activated representations: Adding a piece of evidence from a high-repetition design

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ABSTRACT

The N400 event-related potential could index the activation/integration of representations corresponding to the stimulus or, on the contrary, the inhibition of representations that have been inappropriately activated. To test this alternative, series of 3 words were visually presented to subjects in a relatively rapid succession in order to prevent any disengagement of attention. In one block, participants had to judge whether the meaning of the 1st word was related to that of the 3rd. Representations activated by the 2nd word were thus inappropriate and had to be ignored. In another block, these representations were task appropriate as subjects were asked to decide whether the meaning of the 2nd word was related to that of the 3rd. The new technique of massive repetitions was used in order to obtain early peaking and short lasting N400 effects that would be easier to distinguish from effects on the contingent negative variations (CNVs) triggered by the expectancy of 3rd words. The ERPs elicited by 2nd words were more negative in the N400 time window when their meanings were task inappropriate than when these meanings had to be used. These differences were maximal at the latency of the peak of the N400 deflection rather than at the latency of the maximum of the late positive complex or at that of the CNV. They appeared to be greater at centro-parietal sites and slightly larger over the right than over the left hemiscalp. The results thus bring further support to the idea that N400 processes are of an inhibitory nature.

1. Introduction

Memory representations and their current level of activation are two key concepts of cognitive neuroscience. These concepts are used in all domains, including that of language comprehension. Whether a word occurs in a text or in a speech, it first activates representations corresponding to its elementary physical features, that is, to its visual or auditory characteristics. These activations are thought to allow those of the higher representations corresponding to the word visual or auditory entire form, which could then be followed by the activation of an amodal lexical representation (Lau, Phillips, & Poeppel, 2008). At even higher levels, semantic knowledge (Tulving, 1972) corresponding to this word may then be activated as well as the episode(s) in which this word previously occurred. This semantic and episodic information may then be integrated in the representation of the situation depicted by the text or the speech (Kintsch, 1988).[1] When subjects are asked to perform a particular task during an experiment, these situational representations are likely to include the meaning and relevance of the word as to this task. One can thus speak of task situational representations.

Models of language comprehension also have to include expectations (DeLong, Urbach, & Kutas, 2005) and thus the fact that some of the aforementioned representations may be somewhat activated before the actual word occurs. The processing of that word may then reveal that part or all of these expectations were inaccurate. The system may then dampen their level of activation. In addition, models of language comprehension have to include the fact that the processing of the stimulus also is not entirely accurate. Words (e.g., bribe) have been shown to activate not only their own lexical representations but also those of resembling words (e.g., bride) (Debruille, 1998; Holcomb, Grainger, & O'Rourke, 2002). Hence, they could activate inaccurate semantic and episodic knowledge. Most importantly, the level of

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[1] In the context of an experiment, this situational representation would also code for the nature of the task to be performed and hence, for the value of the stimulus in that task.

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activations of all inappropriate representations may have to be dampened for accurate comprehension. These dampening, or inhibition processes, may also be at stake when information co-occur with the stimulus and is irrelevant for comprehension, such as in a cocktail party where several persons are speaking of different topics (Broadbent, 1957).

There seems to be three ways in which all these activations and inhibitions of representations could be performed. The first, the bottom-up way, is triggered by the sensorial afferences generated by the stimulus occurrence and should include mainly activations. The second, the top-down way, depends on activations of representations of a level higher than the one considered. Finally, the lateral way, includes for instance the spreading of automatic activation to associated or to semantically related concepts (Collins & Loftus, 1975) and reciprocal inhibitions (Gurd & Oliveira, 1996; Watters & Patel, 2002).

Lastly, models of language processing also include integration mechanisms (e.g., Kintsch, 1988). These mechanisms, which bind various representations into a coherent whole, could pertain to all the representations subsumed by a representation of a higher level, such as a representation of the situation that is depicted by the text or the speech considered. These mechanisms could also bind together representations of the same level.

The recording of the electrical activity of the brain during the processing of words has led to the discovery of a particular potential, which has been named the N400, due to its negative electrical polarity and its maximum 400 ms after the onset of the stimulus (for a review, see Kutas, Van Petten, & Kluender, 2006). Many studies have attempted to assess which of the above-mentioned processes it would index. Those pertaining to the representations of the physical features of the stimulus have been discarded because the manipulation of those features, such as the word cases (upper versus lower), does not modulate the amplitude or the latency of this event-related potential (ERP). In contrast, the manipulation of semantic expectations leads to extremely robust N400 effects, a fact in line with all the data showing that this ERP is only elicited by potentially meaningful stimuli. Accordingly, one of the first hypotheses about the nature of the brain processes that generate the N400 has been that of semantic activation (Kutas & Hillyard, 1984). The minimal N400 obtained when the meaning of the word matches expectations (e.g., "paint" when it occurs after "Don't touch the wet…") would reflect the minimal semantic activation that remains to be done when most of the activations have already been carried out by the context. The maximal N400s elicited by words whose meaning was unpredicted ("Don't touch the wet dog") would be due to all the semantic activation that this unpredicted word has to induce.

Several activation hypotheses were later developed. Each one focuses on a particular level of representations. From more elementary to higher levels, one can list, first, the relation of N400s to pre-lexical representations, which have been based on N400 modulations induced by low level (i.e., orthographic) manipulations (Deacon, Dynowska, Ritter, & Grose-Fifer, 2004; Deacon, Hewitt, Yang, & Nagata, 2000). Then, comes the relation between N400s and lexical *access*, based, among other things, on the N400s elicited by pseudo-words (e.g., toble) (Kutas & Federmeier, 2011). Another lexical has been proposed by Lau et al. (2008) according to which N400 processes perform the *activation* of an amodal lexical representation of the stimulus, which can also be pre-activated by the preceding context in a top-down way. Meanwhile, the possibility that the N400 could index lateral activations within the lexicon itself, that is, the automatic spreading of activation from one lexical representation to others, was already evoked by Kutas and Hillyard (1984). Finally, N400 has also been related to a level higher than that of the lexicon, namely to the retrieval of world *knowledge* related to lexical representations (e.g., for the lexical entry "dog" the knowledge that a dog is a common four-legged pet mammal) (e.g., Chwilla & Kolk, 2005).

Quite different from all these activation hypotheses is the idea that N400 indexes the *integration* of the meaning of the word in its global context to form a representation of the situation depicted by the text (e.g., St George, Mannes, & Hoffman, 1994; Van Berkum, Hagoort, & Brown, 1999). This hypothesis is based, for instance, on the N400 elicited by a word ending a paragraph, which depends not only on words that immediately precede but also on words that were at the very beginning of that paragraph. The integration idea has also been supported by results of lexical decision studies using trials simply made of a prime and a target word (Chwilla, Hagoort & Brown, 1998).

In order to take into consideration the data used to support these different theories, we propose that N400 processes affect representations at all levels, that is, from the situational to the orthographic level. This idea is included within a theoretical framework in which fast bottom-up processes triggered by the stimulus preconsciously activate representations of all levels and where the lateral reciprocal inhibitions occurring at the highest level would result in the selection of only one situational representation (Debruille, 2007; Debruille et al., 2008). Top-down processes initiated from that highest-level representation would then increase the level of activation of all the lower levels representations it subsumes, enabling them to dampen rival representations by lateral inhibitions at their respective level. N400s would index all these lateral inhibitions, whether they affect representations activated by previous context (i.e., expectations), by the stimulus itself or by co-occurring stimuli. Integration processes would then bind the representations that have not been inhibited into a coherent whole. These remaining representations would then reach a peak level of activation, which could be indexed by the P600, the potential that follows the N400. This would correspond to the conscious perception of the meaning of the occurrence of the stimulus in its context, bound with the awareness of all lower levels.

Three studies were run to test the idea that N400 indexes inhibition processes (Debruille, Pineda, & Renault, 1996; Debruille, 1998; Debruille et al., 2008). The results supported inhibition and were inconsistent with some of the other N400 hypotheses. The 1st and the 2nd of these studies pertained to the inhibition of representations of resembling items that are inappropriately activated by the stimulus (i.e., faces of known people that resemble unknown faces in the 1st study and words that resembles the stimulus word in the 2nd). The last of these three studies (Debruille et al., 2008) explored a particular situation in which the accurate representations of the stimulus were irrelevant to the task but had the characteristics of task-relevant stimuli. As such, they should activate two situational representations: one coding their task irrelevance and one coding inappropriate task-relevance. A competition between these two rival and incompatible representations should occur via reciprocal inhibition. The task-relevant situational representation should be inhibited (which would generate N400 activity). Because of that inhibition, it would not be able to send top-down signals boosting the level of activation of the accurate stimulus representations. Such top-down signals would be sent from the situational representation coding for task irrelevance, a representation likely to be much less active than the task relevant one. These top-down signals would thus be weak and unable to prevent stimulus representations from being laterally inhibited, which would generate additional N400 activity.

To test this prediction of greater N400s for task irrelevant than for task relevant stimuli, the experiment included critical words that had to be ignored in one block and remembered in another block. These critical words were presented during an explicit semantic task, which had to be performed on two words that immediately followed each of them. This task was chosen to increase the odds that critical words would be fully processed and activate representations of all levels, even when participants had to ignore them. Sequences of three words were thus presented visually. To prevent participants, in the ignore block, from starting to focus their attention only on the 2nd words, the stimulus-onset asynchrony (SOA) between 1st and 2nd words was set to be somewhat short (i.e., 600 ms). In accordance with the prediction, ERPs elicited by 1st words were found to be more negative in the N400 time windows when subjects had to ignore critical words than when they had to pay attention in order to be able to report them, which was the memory task used as a control.

This previous study also included a second experiment, which used the same stimulus set. However, the new participants were only asked to judge the semantic relatedness of 2nd and 3rd words. They were not given any instructions regarding 1st words. These subjects were then sorted into a poor- and a good-ignorer group. The poor ignorers were participants who took much longer to judge 2nd–3rd word relatedness when 1st words were misleading, that is, when their meaning was related to that of the 3rd words. In contrast, the good-ignorers were participants who were less affected by this latter relation and were therefore assumed to possess stronger active inhibition processes. In keeping with the N400 inhibition idea, ERPs to 1st words were more negative in the N400s time window in good- than in poor-ignorers. Interestingly, the activation and the integration accounts of the N400 lead to opposite predictions. According to these hypotheses, N400s should have been a) smaller for stimuli that had to be ignored than for those that had to be remembered and b) larger in subjects in whom the meanings of 1st words were processed and affected the semantic processing of adjacent stimuli. The experimental design used was thus found interesting to test various N400 hypotheses.

The aim of the present study was to replicate and extend these findings. We reasoned that more demonstrative data could be obtained if critical words were those in the second position of the triplets, thus when subjects already started to focus their attention and would be least likely to disengage it. The critical task was thus to decide whether the meaning of the 1st word was related to that of the 3rd and thus to ignore 2nd words. The control task was to decide whether the meaning of this 2nd word was related to that of the 3rd. Because of its focus on meaning, this control task was assumed to boost semantic activations and thus to provide a better contrast with the critical task than the memory task used as a control in the above-mentioned study. The new design also suppresses the difficulty of having to perform two different tasks at each trial in the control condition (i.e., the semantic judgment and the memorization). It also rules out the possibility of an account of the more positive ERPs elicited in the N400 time window by the to-be-remembered distractor in terms a Dm effect (Paller, Kutas, & Mayes, 1987). On the other hand, in the previous study, due to the relatively short SOAs adopted, there was an overlap of the N400s with the contingent negative variations (CNVs) triggered by the expectancies of the 2nd words. To interpret the more negative ERPs obtained in the N400 time window as actually due to greater N400 potentials (rather than to greater CNVs), it was necessary to use CNV data from previous literature (Holcomb, 1988; Koyama, Nageishi, & Shimokochi, 1992). In the present study, we attempted to circumvent this problem by using a massive repetition paradigm. Indeed, in such designs, N400 deflections and N400 effects peak about 100 ms earlier and last shorter (Debruille & Renoult, 2009; Renoult, Brodeur, & Debruille, 2010; Renoult, Wang, Mortimer, & Debruille, 2012; Renoult, Wang, Calcagno, Prévost & Debruille, 2012). They take place in a 260–340 ms time window instead of the 300–500 ms time-window of classical N400 paradigms. In these new paradigms, the peak of the N400 effects should thus clearly precede the maxima of the CNVs and of CNV effects.

Incidentally, it has to be noted that, in the semantic tasks used in these massive repetitions experiments, the amplitudes and the scalp distributions of N400 effects were stable across various repetition levels (e.g., Renoult, Wang, Calcagno, Prévost & Debruille, 2012). This stability raises two important points. First, the particular processes indexed by N400 potentials may be studied at high repetition rates. Second, N400 processes cannot be directly related to the conscious feelings of the meaning of a word. Indeed, with such massive repetitions, this feeling notably decreases, a phenomenon known as semantic satiation. The stability of N400 effects may also question the views that N400 indexes processes of access or of activation of stimulus representations (whatever the level these representations). Indeed, when only two words are used as targets, their representations are likely to be maximally activated during the entire experiment. There might thus be no difficulty at accessing these representations and no further activation and integration effort needed.

For the purpose of the current study, francophone participants were presented with two blocks of trials, each corresponding to one particular task instruction, as in the previous experiment Each trial also consisted of a brief three-French-word sequence. As mentioned, the critical task was to determine whether or not the 1st word was semantically related to the 3rd, thereby ignoring the 2nd word. We called this task the "1–3 task". The control task of determining whether or not the 2nd word was semantically related to the 3rd was called the "2–3 task". Importantly, only twelve unique three-word sequences were presented to each participant, each repeated twenty-five times per block. The stimuli used for both blocks/tasks were the same within one subject, but varied across subjects. In this context, we studied the ERPs evoked by the 2nd words according to whether subjects had to ignore them or to use their meanings to compare them to those of the 3rd words. If the N400 indexes inhibition, 2nd words that have to be ignored should elicited N400s of larger amplitude than 2nd words whose meanings have to be used. In contrast, if N400 indexes integration or the access to or the activation of representations of the 2nd words, larger N400s should be elicited when subjects have to use the meaning of the 2nd words to decide whether it is related to that of the 3rd word than when participants have to ignore these 2nd words.

2. Methods

2.1. Participants

Twenty-four right-handed participants for whom French was the mother tongue were recruited through newspaper advertisements. One participant did not complete the study. Three participants had error rates above 10% in their responses and were therefore excluded from analyses. Our final sample thus consisted of 20 participants. All had normal or corrected-to-normal vision and no history of neurological or psychiatric disorders. They were aged from 18 to 35 (mean 27.7, SD 5) and had all completed high school. Their mean number of years of education was 15.6 (SD 1.8). All participants signed an informed consent form accepted by the Douglas Hospital Research Ethics Board.

2.2. Stimuli

Eleven sets, each including twelve three-words sequences, were used across participants. No stimulus set was used for more than three participants. Each participant was presented with the same stimulus set twice: once for the 2–3 task, and once for the 1–3 task. Each three-words sequence (triplet) represented a unique condition used in 25 trials, for a total of 300 trials per set and task. Amongst the 12 word triplets, there were two possible 1st words, two possible 2nd words and 12 possible 3rd words. Each 1st word and each 2nd word were thus used in six conditions. The composition of one of our 12 stimulus sets is presented as an example in an event tree with english translation of the French words used (Fig. 1). Each of the twelve conditions had a specific pattern of relationships between the three words. These relationships are given in Table 1.

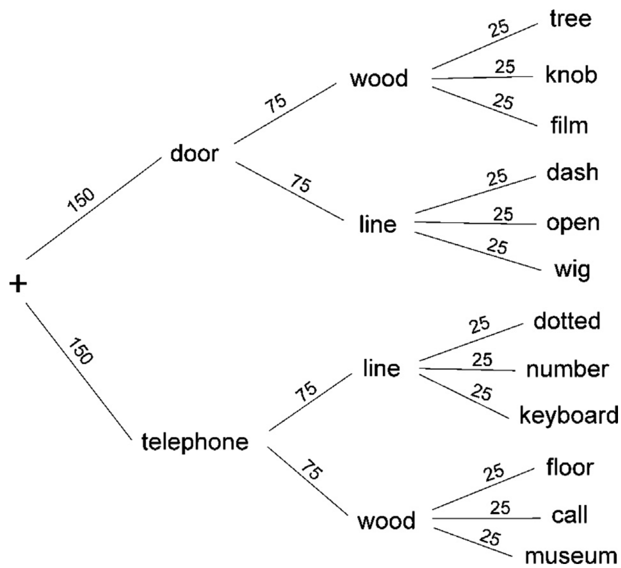

Fig. 1. Event tree representing the various word combinations appearing in one of the eleven stimulus sets. Numbers on connecting lines indicate number of trials per block.

Table 1
Semantic relatedness between words in each condition. These example words are English translations. Original words were in French. Each condition included 25 trials. Note that in the first condition, where 1st words were related to 2nd words and 2nd words were related to 3rd words, 1st words were indirectly related to 3rd words rather that unrelated.

Condition	Example 1st word	Example 2nd word	Example 3rd word	1–2 Related?	2–3 Related?	1–3 Related?
1	Door	Wood	Tree	Yes	Yes	No
2	Door	Wood	Knob	Yes	No	Yes
3	Door	Wood	Film	Yes	No	No
4	Door	Line	Dash	No	Yes	No
5	Door	Line	Open	No	No	Yes
6	Door	Line	Wig	No	No	No
7	Telephone	Line	Dotted	Yes	Yes	No
8	Telephone	Line	Number	Yes	No	Yes
9	Telephone	Line	Keyboard	Yes	No	No
10	Telephone	Wood	Floor	No	Yes	No
11	Telephone	Wood	Call	No	No	Yes
12	Telephone	Wood	Museum	No	No	No

Because our hypothesis pertains to the effect of task, which only requires comparison of the ERPs elicited by the 2nd words between two blocks that were identical in terms of stimuli, there was no need to choose stimuli whose lexical frequency or length would be matched across the twelve conditions. However, since we also report the effect of match on the 3rd words, we analyzed these variables for these 3rd words and compared the conditions where the first stimuli on focus (that is, the 1st word in the 1–3 task and the 2nd word in the 2–3 task) semantically matched the 3rd words to those where they did not match. For lexical frequency, we performed a one-way ANOVA on the logarithm of the mean number of occurrences per 100 million words. These data were acquired from the Brulex database (Content, Mousty, & Radeau, 1990). For the 2–3 task, the mean frequency of 3rd words in the match condition was 3.4 (SD: 0.8). In the mismatch condition, it was 3.3 (SD: 0.7). In the 1–3 task, these numbers were 3.5 (SD: 0.7) and 3.3 (SD: 0.7). No significant difference was found. Similarly, no significant difference was found in word lengths measured as the number of letters.

2.3. Procedure

Participants were seated in a dimly-lit sound-attenuated room and were instructed to fixate the center of a computer screen located 0.8 m from their eyes. The word stimuli were black on a white background and displayed in 24 point Boston typeface. Each trial consisted of three words presented serially, followed by a blink instruction. The sequence and timing of their presentation is presented in Fig. 2.

As in the previous study (Debruille et al., 2008), the stimulus onset asynchronies (SOAs) between the three words were chosen to be short enough (i.e., 600 ms) to prevent participants from using simple attention-based strategies for attending or ignoring words (that is, to engage and disengage attention). On the other hand, these 600 ms SOAs were chosen to be long enough so that the entire N400 could develop before the onset of the next stimulus. To further ensure that the participants' attention was focused throughout the task, a fixation cross appearing at the center of the screen immediately preceded the 1st words, announcing the beginning of the trial. All three words were then presented at the same location on the screen.

Following the application of EEG electrodes, participants were asked to respond as quickly and as accurately as possible by pressing either the right arrow key or the down arrow key of a standard PC keyboard using their right index finger. The assignment of keys to responses (affirmative or negative) was counterbalanced across participants. Participants completed two tasks. In the 2–3 task, they were asked to judge whether the meaning of the 2nd word was related to that of the 3rd word in each three word sequence. This was accompanied by an instruction to ignore the 1st word. In the 1–3 task, participants were asked to judge whether the meaning of the 1st word was semantically related to that of the 3rd word and to ignore the 2nd word. They were asked to blink only at the blink stimuli. Every participant performed both tasks, the order of which was counterbalanced across subjects.

2.4. Data acquisition

The nature and the timing of the response to each target word were recorded. The EEG was captured with tin electrodes mounted in an elastic cap (Electrocap International) from 26 active points placed according to the extended International 10–20 System. They were grouped in a sagittal (Fz, Fcz, Cz & Pz), a parasagittal (Fp1/2, F3/4, Fc3/4, C3/4, Cp3/4, P3/4 & O1/2) and a lateral (Ft7/8, T3/4, Tp7/8 & T5/6) subset and referenced to an electrode placed on the left ear lobe. Impedances were kept below 5 kΩ. Vertical eye movements were monitored by an additional electrode placed below the right eye. EEG signals were amplified 20,000 times. We set high and low pass filter half-amplitude cut-offs at.01 and 100 Hz using an additional 60 Hz electronic notch filter. Signals were digitized on-line at a sampling rate of 512 Hz and stored along with stimulus and response codes for subsequent averaging.

2.5. Data processing

Prior to averaging, we used an algorithm to reject trials with excessive eye movements (EOG) as well as muscle artifacts (EMG) greater than $+100\,\mu V$ or smaller than $-100\,\mu V$. Channels with amplifier blocking or analog to digital clipping lasting more than 100 ms were also rejected. Trials in which participants gave an incorrect response, no response, or a response faster than 200 ms or slower than 2000 ms after the onset of the 3rd word were discarded. In addition, the first 25 trials in each block were rejected, as early trials were those in which participants were getting accustomed to the repetition. The aim of this latter rejection was to use only those trials in which repetition does not produce further decreases of N400 amplitudes (Renoult, Wang, Calcagno, Prévost, & Debruille, 2012). Averages were first calculated for each condition (as in Table 1) of each task. Averages of these averages were then computed for the contrasts described in Section 3 of this article.

2.6. Measures and statistics

Mean reaction times to 3rd words were compared between the 2–3 task and the 1–3 task using a one-way ANOVA with task (1–3 vs. 2–3) as a within subject factor. The match factor was not used as, for 3rd words, there were twice as many mismatches as there were match trials. Mean voltage ERP amplitudes were computed relative to a 200 ms baseline established before the 2nd and then, before the 3rd words. The time windows in which these mean voltage amplitudes were computed were: 100–200 ms for the N1s, 260–340 ms for the N400s, 350–450 for the late positive complex (LPC) and 450–600 ms for the contingent negative variation (CNV). The N1 time window was designed to broadly encompass the N1 deflection (Mangun & Hillyard, 1995) for which unexpected differences were detected by visual inspection. The N400 time window was chosen based on the peak of the negative-going deflection that appeared after the N1 in our grand averages. This second negative deflection peaked at approximately 300 ms at Cz as in (Debruille & Renoult, 2009). Narrow limits of 40 ms on each side of this latency were adopted to capture it precisely. The limits of the time windows of the LPC and of the CNV were chosen to analyze the last portions of the ERPs, that is, those preceding 600 ms. Electrophysiological data were compared using repeated-measures ANOVAs including, in addition to the task and the semantic match factor, the electrode factor in the ANOVA used for the sagittal subset and a fourth factor, hemiscalp (right vs. left), for the ANOVAs for the parasagittal and the lateral subset. Results are reported with the original degrees of freedom and the p values corrected by Greenhouse and Geisser (1959) technique for lack of sphericity.

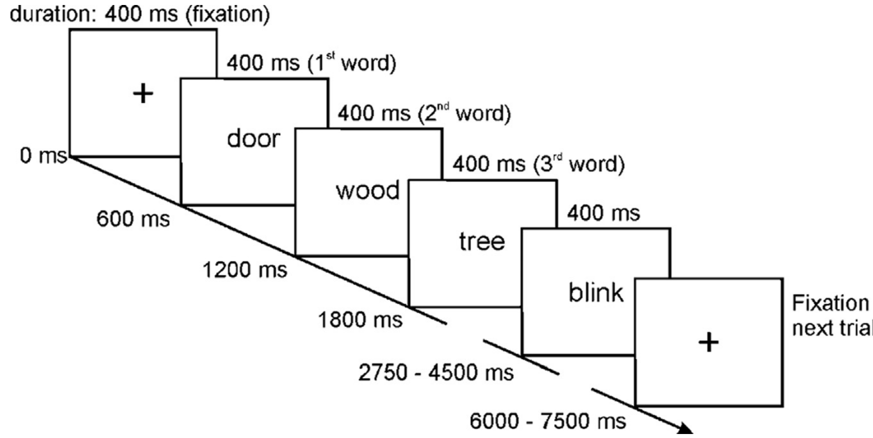

Fig. 2. Stimulus sequence and timing in each trial. The inter-trial interval was varied randomly between 6000 ms and 7500 ms.

Table 2
Mean reaction times for 3rd words in each condition and in each task.

1–2 Related?	2–3 Related?	1–3 Related?	2–3 Task (SD)	1–3 Task (SD)
Yes	Yes	No	756 (2 1 6)	804 (2 4 8)
Yes	No	Yes	813 (2 5 1)	750 (1 9 9)
Yes	No	No	694 (1 7 4)	694 (172
No	Yes	No	759 (2 0 2)	774 (2 2 8)
No	No	Yes	773 (2 2 8)	757 (2 2 2)
No	No	No	703 (1 8 2)	699 (1 6 0)

3. Results

3.1. Behavioral data

Response times for the 3rd words of the 2–3 task (mean 749 ms) were almost identical to response times for the 1–3 task (mean 746 ms). The effect of semantic matching was not studied as there were twice as many trials that required a "no" response than trials that required a "yes" response" (Table 1), which could shorten response times to mismatching 3rd words. We are thus just providing results in Table 2. As in the previous study, RTs appeared long in case of "contradictions". Here, this was in the 1–3 task when the 1st word was not related to the 3rd whereas the 2nd was (804 ms when the 1st word was related to the 2nd and 774 ms when the 1st was not related to the 2nd) and in the 2–3 task, when the 2nd word was not related to the 3rd whereas the 1st was (813 ms when the 1st was related to the 2nd and 773 ms when the 1st was not related to the 2nd). No mean error rate was greater than 3%, some participants making no error at all, probably due to the high repetition rates and the elimination of the first 25 trials of each task.

3.2. Electrophysiological data

3.2.1. Second words

Fig. 3 shows, at the top, the grand average ERPs for the 2nd words in the 1–3 task plotted with those of the 2–3 task and, at the bottom, the subtractions of the latter from the former ERPs. This subtraction includes two main negative components easy to see at Pz. The first is maximal at 150 ms and falls within the N1 time window. The second, maximal at 300 ms post-onset, coincides with the peak of the N400, which can be seen on raw ERPs particularly at Cz. Figs. 4 and 5 show the scalp distributions of these two components, respectively.

In the N1 time window, ERPs appeared more negative when 2nd words had to be ignored than when their meanings had to be taken into account. The ANOVA run for the sagittal subset revealed that these task differences were a trend ($F(1,19)=2.92$, $p=.104$). They were just significant at the parasagittal subset ($F(1,19)=4.67$, $p=.044$) with a trend towards a task x electrode interaction ($F(6,114)=2.57$, $p=.088$, $\varepsilon=.345$). Post-hoc analyses at F3/4 and Fc3/4 electrode locations confirmed an effect of task ($F(1,19)=6.39$, $p=.020$) and ($F(1,19)=7.64$, $p=.012$), respectively. The ANOVA for the lateral subset also showed a (modest) effect of task ($F(1,19)=5.27$, $p=.033$).

In the N400 window, ERPs also appeared more negative when 2nd words had to be ignored than when their meanings had to be taken into account. The analysis made for the sagittal subset revealed an effect of task ($F(1,19)=7.02$, $p=.016$) with a mild trend towards an interaction of task with electrode ($F(3,57)=2.33$, $p=.131$). The ANOVA focused on Pz, the electrode site for an a priori hypothesis for a classical N400 effect with visual words, revealed an effect of task ($F(1,19)=11.9$, $p=.003$). For the parasagittal subset, the ANOVA also showed an effect of task ($F(1,19)=17.164$, $p=.0006$), as well as a trend towards an interaction with hemiscalp ($F(1,19)=3.26$, $p=.087$) in relation to the slightly greater differences observed at right hemiscalp locations. A post-hoc ANOVA at right electrode sites confirmed the effect of task ($F(1,19)=18.7$, $p=.0004$), which was also significant for left electrode sites ($F(1,19)=13.9$, $p=.0014$). At the lateral subset, there was also an effect of task ($F(1,19)=14.6$, $p=.001$) and an interaction of task with hemiscalp ($F(1,19)=5.57$, $p=.029$) in relation to the slightly greater difference observed at right hemiscalp locations. A post-hoc ANOVA at right electrode sites confirmed the effect of task ($F(1,19)=22.6$, $p=.0001$), which was also (modestly) significant at left electrodes ($F(1,19)=4.99$, $p=.038$). No effect of semantic match with the 1st words was found in this N400 time window nor any interaction involving this factor.

In the LPC time window, there was no effect of task for the midline subset but a task x electrode trend ($F(3,57)=2.59$, $p=.090$). For the parasagittal subset, a (modest) task effect was observed ($F(1,19)=4.97$, $p=.038$) together with a task x electrode interaction ($F(6,114)=3.71$, $p=.022$). The ANOVA run for the lateral subset revealed a significant effect of task ($F(1,19)=10.26$, $p=.005$) with no interaction.

In the CNV time window, there was only a trend for task at the lateral subset of electrodes ($F(1,19)=3.33$, $p=.0.84$).

3.2.2. Third words

ERPs to 3rd words were similar across tasks. In contrast, they appeared less negative in the N400 time window when these words semantically matched the prime word on which the subject had to focus than when these words did not match this prime. The grand averages for this contrast are displayed in Fig. 7. Differences were significant at the sagittal ($F(1,19=42.91$, $p<.001$), the parasagittal ($F(1,19=39.45$, $p<.001$) and the lateral subset ($F(1,19=27.02$, $p<.001$).

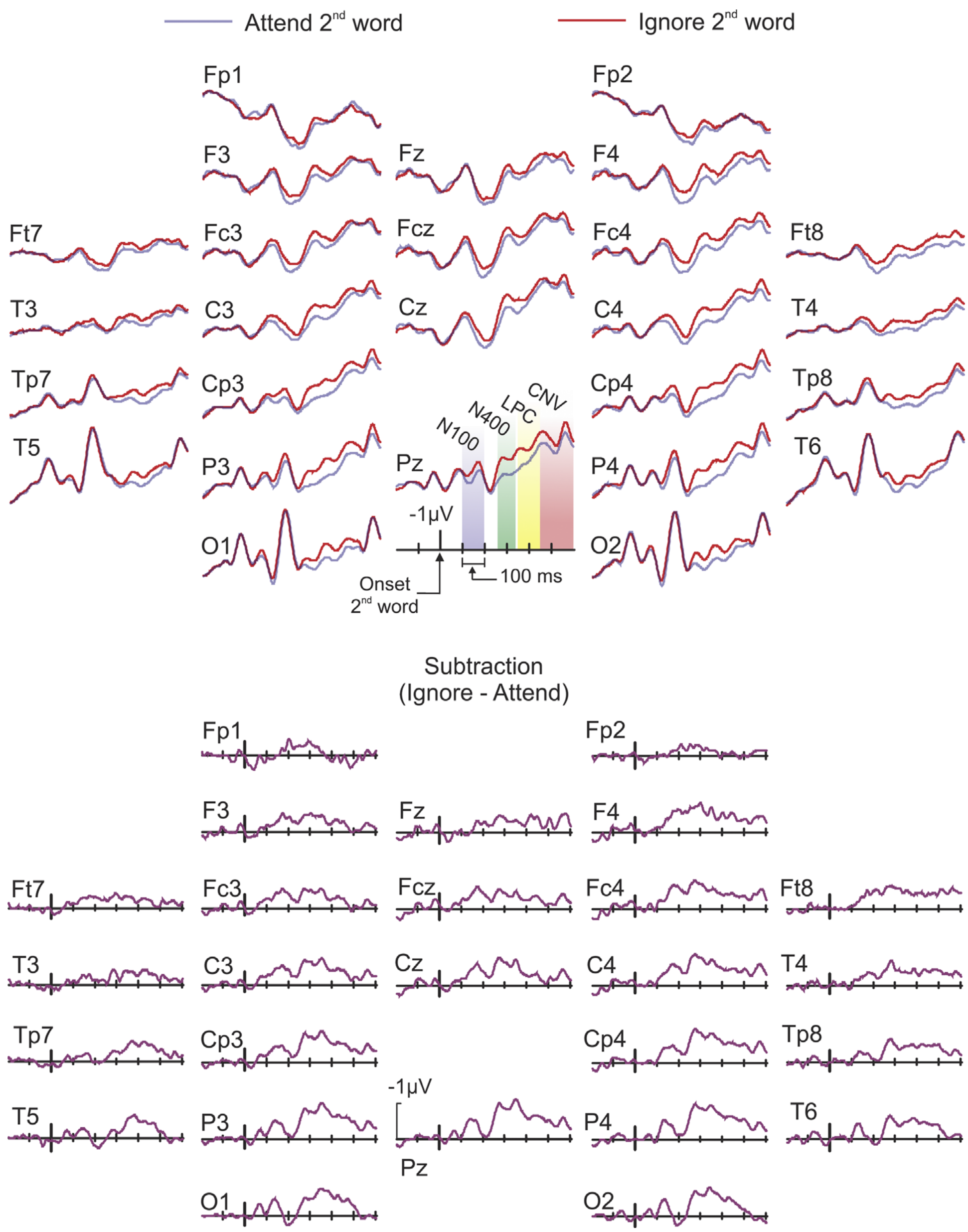

Fig. 3. Top: grand average of ERPs ($n=20$) evoked by the 2nd words of the triplets. Red lines correspond to the ERPs for the 1–3 task, wherein participants had to judge the semantic relationship between the 1st and 3rd words and where the meaning of the 2nd words had to be ignored. Grey lines represent the ERPs for the 2–3 task, wherein participants had to judge the semantic relationship between the 2nd and 3rd words and thus where the meaning of the 2nd word had to be used. Baselines were computed in the −200 ms to 0 ms pre-2nd word-onset time window. Bottom: Subtraction of the ERPs of the 2–3 task from the ERPs of the 1–3 task.

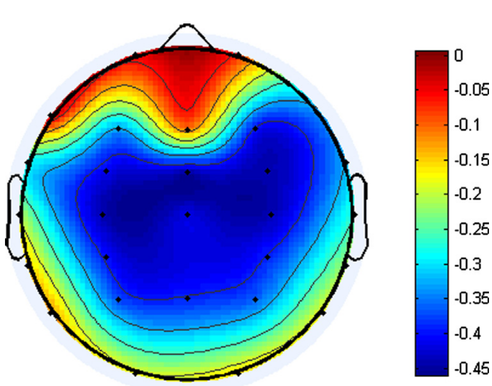

Fig. 4. Spline interpolated isovoltage map of the subtraction of the 2nd word ERPs of 2–3 task from the 2nd word ERPs of 1–3 task (ignore 2nd word) in the N1 time window.

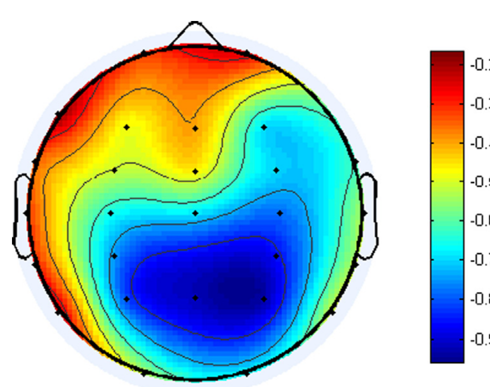

Fig. 5. Spline interpolated isovoltage map of the subtraction of 2nd word ERPs of the 2–3 task from the 2nd word ERPs of 1–3 task (ignore 2nd word) in the N400 time window.

4. Discussion

In the present study, each trial consisted of three written words serially presented to subjects. In one block, they had to judge whether the meaning of the 1st word was related to that of the 3rd (the 1–3 task). In the other block, they had to decide whether the meaning of the 2nd word was related to that of the 3rd (the 2–3 task). Response times of the two tasks were almost identical, suggesting that subjects did not disengage their attention for irrelevant 2nd words in the 1–3 task, which would probably have led to longer response times in that task given that attention would have had to be re-engaged at the occurrence of the 3rd word. In accordance with the idea that N400 is generated by inhibition processes, the ERPs elicited by 2nd words were more negative in the time window of the N400 potential when the meaning of this word was inappropriate to the task than when it had to be taken into account. These results contrast with the ideas that N400s index access, activation or integration processes, which predict larger N400s when subjects have to take into account the meaning of words.

The amplitudes of these ERPs differences were maximal in the time window of the N400 deflection rather than in the time window of the late positive complex (LPC) or at the peak of the contingent negative variation (CNV). They were also maximal at centro-parietal sites and slightly greater over the right than over the left hemiscalp (Fig. 6), as is usually the case with the effect of semantic matching on N400 with visually presented words (Kutas et al., 2006). These results support the idea that the ERP differences obtained were classical N400 effects.

The absence of a N400 semantic matching effect for 2nd words, whereas it was present for 3rd words, is not surprising. Renoult, Wang, Mortimer and Debruille (2012) showed that in order to preserve such N400 effects when stimuli are highly repeated, an explicit semantic matching task is required. Although the present study does contain a semantic task, it is not applied to the matching of the 1st word with the 2nd. The results of the present study thus suggest that semantic matching effects on N400 in high repetition designs could only be obtained for target stimuli. One possibility is that, because of the repetitions, each of the two possible 1st words are closely associated to each of the two possible 2nd words. Consequently, each 1st word would equally activate both 2nd words. When the actual 2nd word occurs, the representation of the other is inhibited, whatever its semantic relation with the 1st word, accounting for the lack of N400 difference. In contrast, in an experiment where such 2nd words are the targets of an explicit semantic task, the semantic relation between the 1st and the 2nd would count, as it corresponds to the task-relevant situational representation.

The next paragraphs are thus devoted to a detailed discussion of the results within the theoretical framework of the N400 inhibition idea. One of the first things that may be discussed is the small size of the *differences* obtained. This cannot be due to the use of a high-repetition protocol since large N400 effects can still be obtained with intense repetition (e.g., Renoult, Wang, Calcagno, Prévost, & Debruille, 2012; Renoult, Wang, Mortimer, & Debruille, 2012). Two facts probably coincided. First and most importantly, the task of ignoring a stimulus that occurs just after and just before words that have to be attended is likely to be a difficult task for subjects to implement. Second, in high-repetition protocols, N400 effects were measured on the ERPs evoked by target words, for which larger N400 effects are usually found. It is possible that N400 effects on 2nd words were small because these stimuli were not targets. Maximal activation and then, inhibition, may occur only for these latter stimuli for which processing should *a priori* be more complete.

Another finding may also appear puzzling at first: the presence of a N400 deflection for 2nd words when their meaning had to be taken into account. According to the hypothesis that N400s are generated by inhibition processes, it seems that these N400s should have been minimal since minimal inhibitions had to be

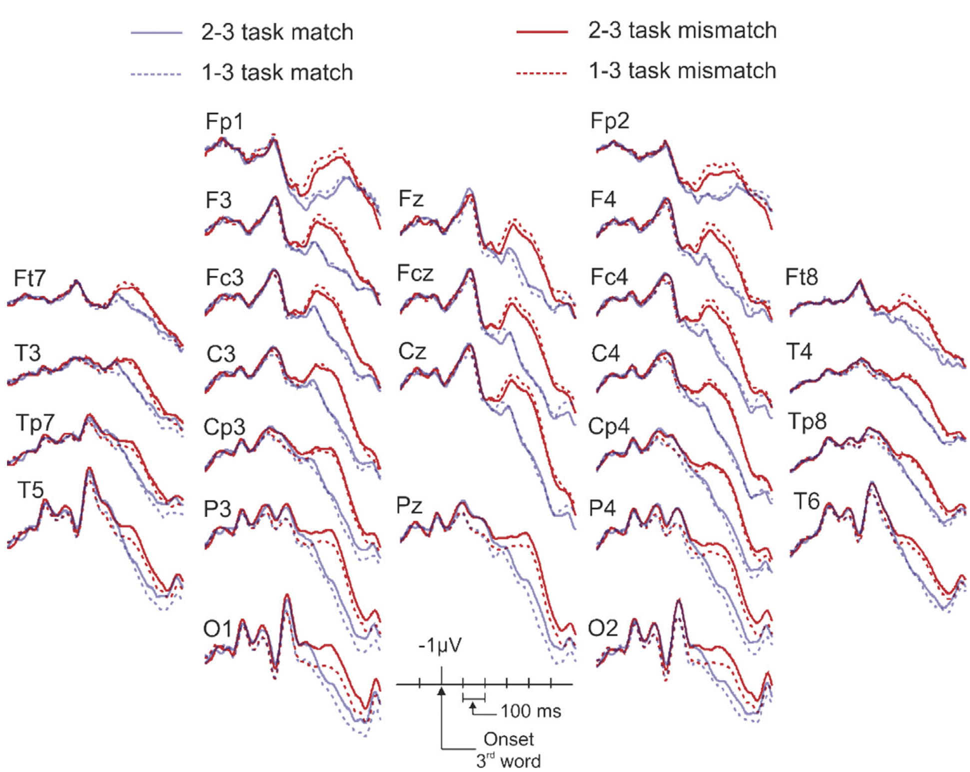

Fig. 6. Grand average of ERPs ($n=20$) evoked by the 3rd words. Doted lines are for the task where subject had to decide whether the meaning of the 1st word was related to that of the 3rd. Continuous line are for the task where subjects had to decide whether the meaning of the 2nd word was related to that of the 3rd word. Blue is for matches and red for mismatches. Baselines were computed in a −200 ms to 0 ms pre-3rd word onset time window.

performed in this case. Nevertheless, in the experimental design, 2nd words could be just one of two possible words. Most likely, both were thus expected and their representations pre-activated. The occurrence of the real 2nd word could thus systematically trigger the inhibition of the representations of the other word, generating these N400 deflections.

The theoretical framework in which the N400 inhibition idea is proposed provides a hypothesis as to the nature of the inaccurate (or inappropriate) representations whose inhibition would be responsible for the additional N400 activity triggered by 2nd words in the 1–3 task relative to the 2–3 task. This hypothesis is based on the likeliness that subjects are building a global representation of the information that is necessary to perform the task and thus a global representation of the two task-relevant words of each triplet and of their relationship. The activations triggered by the 2nd words in the 1–3 task are not subsumed by this global representation, which would thus not send top-down signals reinforcing them. Accordingly, they will be more affected by lateral reciprocal inhibition, which will be indexed by the larger N400s. In contrast, in the 2–3 task, the activations triggered by the 2nd words are subsumed by this global representation, which thus send strong reinforcing top-down signals preventing their inhibition.

Another important question arising is that of consciousness. It seems that if, in the case of the 2nd words of the 1–3 task, accurate stimulus representations lose the reciprocal inhibition competition and are dampened, no conscious perception of these word should occur. This is certainly not the case. Even if these stimuli were not task relevant, they were presented supraliminally. Subjects saw them and were most likely aware of their meanings[2]. One possibility is that inhibition could pertain only to a subset of the stimulus representations activated. For instance, the inhibition could affect only representations underlain by the dorsal stream (Cohen & Andersen, 2002), that is, by the parieto-frontal cortex, which are involved in actions and thus, in the task. Representations underlain by the occipito-temporal neurons of the ventral stream (the 'What' path) might not be affected. This latter path is likely to code the nature of the stimulus and to encode its occurrence in an episodic representation of the event. These latter processes could well occur not only in the cases where the stimulus is relevant for the task but also in the case it is not, accounting for the ability of subjects to remember task-irrelevant material. Accordingly, in the ventral path, there would be a global representation subsuming any event. This global representation would send top-down signals reinforcing the level of activations of accurate representations of the word, accounting for its conscious perception. In contrast, in the dorsal path, such a global representation might not exist and no dorsal top-down signals would be sent. Or, there could be a global dorsal representation coding for task irrelevance that sends top-down signals. These latter signals are likely to be weaker than those sent by task-relevant representations in the case of a task relevant stimulus, as proposed in the Introduction. In both cases, accurate representations activated by the stimulus in these dorsal cortex could thus lose the reciprocal inhibition competition accounting for the additional N400 activity observed for irrelevant 2nd words.

Surprisingly, second words elicited larger visual N1s in the 1–3 than in the 2–3 task. The possibility that the ERP differences occurring in the N400 time window could be due to an effect starting during the N1 time window has to be examined. When looking Fig. 3 at Pz and and P4, the electrodes where the N400 effects were the largest, it seems that there is an absence of ERP difference between those taking place in the N400 time window and the ones occurring during the N1 time window, suggesting that the two effects are separated. Differences waves were computed to check whether this were actually the case. The bottom of Fig. 3 display these differences waves. At Pz and at P4, around 200 ms post onset, there is a clear return to the baseline, clearly revealing an absence of difference between the two time windows. On the other hand, the effect taking place during the N1 time window has a scalp distribution centered between Cz and FCz, as illustrated by Fig. 4. Meanwhile, the effect occurring in the N400 time window is centered between Pz and P4 (see Fig. 5). Thus, both time courses and scalp distributions differ. Accordingly, it seems unlikely that the differences occurring in the N400 time window could be due to an effect starting in the N1 time window.

Together with the larger N400s they evoked, this unexpected N1 finding can be used to show that participants did not pay less attention to 2nd words when they were task irrelevant. The relatively short stimulus-onset asynchrony (SOA) was thus efficient at preventing participants from passively ignoring unnecessary words by simply paying less attention to them. Smaller N1s to 2nd words in the 1–3 than in the 2–3 task would have meant a failure at preventing this type of ignoring. On the other hand, the fact that the exact opposite was found is puzzling. It is reminiscent of the larger N1s of good-ignorers relative to poor-ignorers observed in Debruille et al. (2008). These two results N1s appear at first to be in contradiction with the smaller N1s found for stimuli that are not the focus of attention (Mangun & Hillyard, 1995) relative to stimuli occurring within this focus. However, in the studies summarized in that review, non-attended stimuli are deprived of the elementary features (color, positions etc) that define what should be attended to. This was not the case in Debruille et al. (2008) and in the present study. The N1 results of these latter studies could suggest that active ignorance of stimuli that possess attended features might also trigger some type of N1 processes.

As mentioned, the ERPs elicited by the 2nd words were more negative in the N400 time window in the task that required participants to ignore the 2nd word than in the task that required participants to attend to this word. The maximum of these differences coincide with the timing of the peak of the N400 deflection. It had a centro-parietal distribution with a slight bias towards the right hemiscalp (see Fig. 4) as is typical of the N400 effects obtained with visually presented words (Kutas et al., 2006). The fact that the maximum of the effect was not seen during the time window of the late positive complex (LPC) suggests that the effect cannot be interpreted as a reduction in LPCs due to a lesser attention to the 2nd words that had to be actively ignored. In addition, this view would not be consistent with the fact that these 2nd words elicited greater N1s in the 1–3 task than in the 2–3 task. Likewise, the effect cannot be due to a greater Dm effect for the 2nd words of the 2–3 task (Paller et al., 1987). Indeed, the greater memory encoding indexed by the Dm effect is most unlikely to occur here, where words were presented 150 times in the block. Finally, because of the timing of its maximum and of its scalp distribution, the effect may not be due to greater contingent negative variations to the 2nd words of the 1–3 task than to those of the 2–3 task. CNV effects obtained in short SOA designs are usually maximal around the time of onset of the expected stimuli (here the 3rd words). Results thus replicate and extend those obtained by Debruille et al. (2008) in conditions where their interpretation is clearer. They provide further support to the idea that N400 processes are of an inhibitory nature.

Seemingly, it could still be possible to argue that the N400 indexes access and/or activation processes by assuming that these greater N400s index a greater difficulty at accessing or activating

[2] This is the case for instance in the Stroop effect where the word and its meaning are not relevant for the task-which is only to discriminate whether letters are green of red, for instance- and where the meaning of the word (e.g., RED) is nevertheless consciously perceived.

representations in the conditions in which the meaning of the 2nd word had to be ignored. However, this “difficulty” version of the N400 access and activation hypotheses would predict larger N400s for words in the other tasks that divert attention from the processing of their meaning, such as deciding whether words are written in upper- or lower-cases (e.g., Chwilla, Brown, & Hagoort, 1995), or whether they are written with green or red letters. Nevertheless, this is the opposite of what has been found. In such tasks, words hardly elicit any N400 activity and little or no N400 effect can be found (despite the fact that subjects consciously perceive the meaning of the words presented).

The idea that N400s indexes the integration of the meaning of a word into its context also seems incompatible with the data. It predicts that N400 to 2nd words should have been larger when subjects devoted more efforts at integrating their meaning and thus in the 2–3 task. Given that this was not the case, it could be argued that N400s were larger in the 1–3 task because integration processes encountered more difficulties when participants were asked to ignore the meaning of a word. Nevertheless, this account would also be incompatible with the small size or absence of N400 in studies attempting to divert participants from meaning processing (such as, Chwilla et al., 1995).

In contrast, these data can be made consistent with the theoretical framework of the N400 inhibition idea. They suggest that when the meaning of the word stimulus does not correspond to any task situational representations, there is less reciprocal inhibition and hence, less N400 activity. Meanwhile, the conscious perception of the meaning of the words in these tasks can be accounted for by using the occipito-temporal “What” path, as mentioned above.

Moreover, it may also be concluded that interesting insights on the nature of the computations performed by the brain processes responsible for some ERPs can be derived from protocols requiring active ignorance of stimuli on which attention is focused.

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